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DEVELOPMENT AND ENCAPSULATION OF THE ENDOPARASITOID, *MICROPLITIS CROCEIPES (HYM. : BRACONIDAE)*, IN SIX CANDIDATE HOST SPECIES *(LEP.)*

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Encapsulation and development of the endoparasitoid, *Microplitis croceipes* (Cresson), were studied in six atypical lepidopteran host species whose usual host is *Helicoverpa zea* (Boddie). The candidate hosts examined were : the fall armyworm *Spodoptera frugiperda* (J. E. Smith) ; the beet armyworm, *Spodoptera exigua* (Hübner) ; the cabbage looper, *Trichoplusia ni* (Hübner) ; the greater wax moth, *Galleria mellonella* (L.) ; the Indian meal moth, *Plodia interpunctella* (Hübner) ; and the diamondback moth, *Plutella xylostella* (L.). Both *S. exigua* and *T. ni* were completely unsuitable for *M. croceipes* development due to the high rate of eggs that were encapsulated within three days after parasitism. Encapsulation in *S. frugiperda* included mainly parasitoid eggs and was first detected six days after parasitization at 25 °C and two days at 30 °C. Encapsulation in *G. mellonella* occurred only in the larval stage of the parasitoid. In *P. interpunctella,* parasitoid larvae reached the 3rd stadium, but none of them pupated. Only *S. frugiperda* and *G. mellonella* supported successful development of *M. croceipes* from egg to adult. The percentage of parasitoids reaching the adult stage in these hosts was higher at 30 °C than at 25 °C (13 % vs. 4 % in *S. frugiperda,* and 21 % vs. 3 % in *G. mellonella,* respectively). However, these percentages were too low to substitute them as a more economical host for rearing *M. croceipes.* This biological information will be useful in additional laboratory studies directed toward reducing the rate of encapsulation (e.g., manipulation of host rearing temperature) to increase production of *M. croceipes* on these hosts.

KEY-WORDS : Host suitability, parasitoid encapsulation, development, *Microplitis croceipes, Spodoptera frugiperda, Galleria mellonella, Spodoptera exigua, Plodia interpunctella, Plutella xylostella, Trichoplusia ni.*

Microplitis croceipes (Cresson) is a solitary and specific endoparasitoid of larvae of *Heliothis/Helicoverpa* spp., and is native on two of the most economically important pests in the United States, *Helicoverpa zea* (Boddie) and *Heliothis virescens* (F.) (Lewis & Brazzel, 1966 ; Mueller & Phillips, 1983 ; King *et al.,* 1985 ; King & Coleman, 1989). High rates of parasitism of *H. zea* and *H. virescens* have been reported in cotton (Snow *et al.,* 1966 ; King *et al.,* 1985 ; Powell & King, 1984) and soybeans (Zehnder *et al.,* 1990).

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The parasitoid also has a high tolerance to commonly used insecticides, especially synthetic pyrethroids (Powell *et al.,* 1986), and so may be useful in potential for the biological control of *Heliothis* species (Knipling & Stadelbacher, 1983).

One possibility for enhancing biological control of *Heliothis/Helicoverpa* spp. is through the inundative release of *M. croceipes.* However, the mass propagating of *M. croceipes* is an important obstacle. Currently, rearing *M. croceipes* in large quantities is expensive, because its hosts, *H. zea* and *H. virescens,* are cannibalistic and must be reared in individual cells (Greany *et al.,* 1984). In addition, no hymenopterous larval endoparasitoid has ever been reared from egg to adult *in vitro* (Grenier *et al.,* 1994) and *M. croceipes* has been reared only to the first instar (Ferkovich *et al.,* 1994). An alternative approach to rearing *M. croceipes* would be to find a host upon which the parasitoid could be reared more economically.

We report herein on the development of *M. croceipes* in six atypical, candidate host species, as well as on the hosts' hemocytic response to the parasitoid.

MATERIALS AND METHODS

The atypical hosts examined were : *Spodoptera frugiperda* (J. E. Smith), *S. exigua* (Hübner), *Trichoplusia ni* (Hübner), *Galleria mellonella* (L.), *Plodia interpunctella* (Hübner), and *Plutella xylostella* (L.).

Host larvae (third-fourth instars) that were not previously exposed to parasitoids were placed in Petri dishes with female wasps (10 host larvae/5 females) for 1 h. To induce female parasitoids to attack the atypical hosts, the larvae were treated with frass plus hemolymph from *H. zea.* Each host was rolled in a drop of hemolymph from 4th instar larvae of *H. zea* and immediately exposed to the female parasitoids. Frass was smeared on the bottom of the Petri dish. Parasitoid females do not paralyse their host. Therefore, after parasitism, the host larvae remain active but do not continue normal growth and development. All host larvae were dissected in a drop of IPL-52B tissue culture medium (GibcoBRL, Grand Island, NY) on a glass slide under a binocular microscope. The wasp eggs or larvae were easy to locate as they usually floated out of the host's hemocoel. Host larvae were considered parasitized only if they contained one or more parasitoid egg(s) or larva(e). Encapsulated eggs and/or larvae were also easily detected. In some cases, larvae were observed to be partially encapsulated and were counted and included with the totally encapsulated larvae. At various times after parasitization the following variables were determined in each parasitoid-host interaction : (1) percentage of hosts with one or more eggs per host ; (2) percentage of parasitoid eggs that had reached germ band stage 24-28 h after parasitization (Counce & Waddington, 1972 ; Ferkovich & Oberlander, 1991) ; (3) encapsulation frequency of parasitoid eggs and larvae ; and (4) presence of live and/or dead parasitoid larvae in parasitized hosts. Also, some hosts were held for several weeks after being parasitized to determine whether the parasitoid third instar larva, after emerging from the host, would pupate and complete development to the adult stage. Similarly, the duration of parasitoid development in the atypical host, *G. mellonella* was compared with that in the typical host, *H. zea.* The effect of the rearing temperature (25° and 30 °C) on parasitoid encapsulation and development also was studied.

Data on parasitoid encapsulation were subjected to ANOVA after arc-sin transformation, and significance between treatments was determined by Neuman-Keuls' multiple-range test (Steel & Torrie, 1960).

RESULTS

DEVELOPMENT OF PARASITOID EGGS

The percentages of *M. croceipes* eggs that reached the germ band stage during the 1st and 2nd day after parasitization varied considerably among the different unusual hosts studied (table 1). At 25 °C and 30 °C, it was highest in *G. mellonella* and *P. interpunctella,* and like that in the typical host, *H. zea* (99.7 %) ; it was moderate in the *T. ni, S. exigua,* and *P. xylostella* at 25 °C (40-87 %) ; and in *T. ni* and *P. xylostella* at 30 °C (44-85 %) and lowest in the *S. frugiperda* at 25 °C (22 %) and in *S. exigua* and *S. frugiperda* at 30 °C (12-17 %).

TABLE 1

Egg development of M. croceipes *in different host species*

Host	Temperature (°C)	Number of parasitized hosts dissected	Parasitoid eggs	
			Total observed	% developed to germ band stage in 1-2 d
H. zea	25	42	302	99.7
	30	40	300	99.7
G. mellonella	25	35	67	100
	30	37	63	100
P. interpunctella	25	18	37	100
	30	22	37	95.0
P. xylostella	25	41	114	86.8
	30	20	47	85.1
T. ni	25	128	216	40.3
	30	60	112	43.8
S. exigua	25	128	167	49.1
	30	98	89	12.4
S. frugiperda	25	103	311	22.2
	30	95	269	17.4

PARASITOID ENCAPSULATION

No eggs or larvae of *M. croceipes* were encapsulated by the two typical hosts, *H. zea* and *H. virescens* (table 2). Likewise, encapsulation was not detected in the two atypical hosts *P. interpunctella* and *P. xylostella.* However, encapsulation (complete or partial) of parasitoid eggs and/or larvae did occur in *S. exigua, T. ni, S. frugiperda,* and *G. mellonella,* and was affected by the rearing temperature in some cases. Encapsulation frequency in *S. exigua, T. ni,* and *S. frugiperda* increased with time (1-8 days) after parasitism.

In *S. exigua,* 100 % of all parasitoid eggs found in host larvae were encapsulated three days after parasitism. In *T. ni,* the rate of encapsulation was lower, but included both

TABLE 2

Encapsulation of M. croceipes *by four atypical host species*

Host	Temperature (°C)	Days after parasitization	Total number of: Parasitized hosts dissected	Total number of: Parasitoid eggs and/or larvae	Percent encapsulation of (Mean ± S.D.): Eggs	Larvae	Total[1]
S. exigua	25	1	195	367	21.8 ± 9.8	0	21.8 ± 9.8[a]
		2	89	165	44.3 ± 29.5	0	44.3 ± 29.5[b]
		3	50	64	100.0 ± 0	0	100.0 ± 0[c]
	30	1	60	106	33.8 ± 11.8	0	33.8 ± 11.8[ab]
		2	39	71	77.3 ± 14.3	0	77.3 ± 14.3[c]
		3	18	23	100.0 ± 0	0	100.0 ± 0[c]
T. ni	25	1	75	136	4.1 ± 3.8	0	4.1 ± 3.8[a]
		2	53	80	19.3 ± 7.5	8.3 ± 7.4	27.6 ± 2.4[b]
		3-4	45	61	43.4 ± 21.2	28.0 ± 15.4	71.3 ± 16.4[d]
	30	1	29	67	8.7 ± 2.0	0	8.7 ± 2.0[a]
		2	31	45	27.6 ± 17.9	22.0 ± 7.7	49.6 ± 10.6[c]
		3-4	22	26	40.6 ± 11.8	46.4 ± 22.7	87.0 ± 11.6[d]
S. frugiperda	25	1	59	170	0	0	0
		2	44	141	0	0	0
		4	30	56	0	0	0
		6-8	64	113	57.2 ± 15.9	1.8	59.6 ± 17.0[b]
	30	1	59	183	0	0	0
		2	36	86	1.2	3.5	2.4 ± 42[a]
		4	49	113	27.3 ± 20.6	0	27.3 ± 20.6[ab]
		6-8	60	89	46.8 ± 32.7	0	46.8 ± 32.7[b]
G. mellonella	25	1-10	64	74	0	0	0
		14-19	39	41	0	21.5 ± 32.4	21.5 ± 32.4[a]
		21-27	35	37	0	45.3 ± 22.0	45.3 ± 22.0[a]
	30	2-15	65	91	0	0	
		17-24	44	47	0	47.5 ± 16.1	47.5 ± 16.1[a]

parasitoid eggs and larvae. In both *S. exigua* and *T. ni,* encapsulation, in most cases, increased significantly with the time after parasitization and with the higher rearing temperature at 30 °C.

In *S. frugiperda* and *G. mellonella,* encapsulation frequency was lower than in *S. exigua* and *T. ni.* In *S. frugiperda,* encapsulation included mostly parasitoid eggs and was first detected 6 days after parasitization at 25 °C, and after two days at 30 °C. Encapsulation in *G. mellonella* was not observed earlier than 14 days after parasitization at 25 °C and 17 days 30 °C, and only parasitoid larvae (1st and 2nd instar) were encapsulated.

Incomplete encapsulation, in which parasitoid larvae were only partially surrounded by host hemocytes, was sometimes observed in larvae of both *S. frugiperda* and *G. mellonella.*

DEVELOPMENT OF PARASITOID LARVAE

Different larval stages of *M. croceipes* were dissected from larvae of *T. ni, G. mellonella, P. interpunctella,* and *P. xylostella* (table 3). No *M. croceipes* larvae were ever found in

S. exigua, probably because of the thorough encapsulation of parasitoid eggs that occurred in this host within three days after parasitism.

In *T. ni,* a few parasitized eggs hatched in their hosts 2-4 days after parasitism. However, no adult wasps, ever emerged from parasitized larvae of *T. ni.*

TABLE 3

Percentage of living or encapsulated larvae of Microplitis croceipes *found in dissected parasitized larvae of five atypical host species*

Host	Temperature (°C)	Days after Parasitization	Total number of		Percent parasitoid larvae (Instar)					
			Parasitized hosts dissected	Parasitoid larvae	Live			Dead (not encapsulated)		
					1st	2nd	3rd	1st	2nd	3rd
T. ni	25	2-4	98	141	21.3	0	0			
	30	2-4	53	71	11.3	0	0			
S. frugiperda	25	2-8	138	310	3.2	1.3	0			
	30	2-8	145	288	6.6	2.4	0.3			
G. mellonella	25	2	35	66	57.6	0	0	42.4	0	0
		9-10	29	37	97.3	2.7	0	0	0	0
		14-19	39	41	29.3	34.1	2.4	2.4	4.9	0
		21-27	35	37	8.1	13.5	0	13.5	16.2	0
	30	2	37	63	60.3	0	0	39.7	0	0
		10	13	13	0	76.9	23.0	0	0	0
		13-15	15	15	0	40.0	46.7	0	13.3	0
		17-24	44	47	2.1	6.4	14.9	0	19.1	8.5
P. interpunctella	25	3	23	47	48.9	0	0	21.3	0	0
		19-22	10	10	0	40.0	60.0	0	0	0
P. xylostella	25	2	15	15	13.3	0	0	86.7	0	0

In *S. frugiperda,* 4.5 % live first and second instar parasitoid larvae at 25 °C, and 9.3 % first, second and third instar larvae at 30 °C, were found 2-8 days after parasitism.

In *G. mellonella,* all parasitized hosts dissected 2 days after parasitism, at either 25° or 30 °C, contained at least one live first instar parasitoid. Hosts that had more than one parasitoid larva/host also had a higher parasitoid mortality rate (40-42 %). Live parasitoid larvae of different stages, were dissected from parasitized hosts at various times after parasitism. More live parasitoid third instars were found at the same time after parasitism at 30 °C than at 25 °C.

In *P. interpunctella,* live first instars of *M. croceipes* were dissected 3 days after parasitism at 25 °C. At that temperature, some live parasitoid second and third instars were dissected from parasitized hosts after 19-22 days. However, no parasitized hosts held for that period or longer yielded any parasitoid pupae.

In *P. xylostella,* all parasitized hosts dissected 2 days after parasitism contained *M. croceipes* first instars but most (87 %) were dead. Other parasitized *P. xylostella* hosts held for possible parasitoid development did not produce any *M. croceipes* cocoons.

PUPATION AND ADULT EMERGENCE

Complete development of *M. croceipes* was recorded only in *S. frugiperda* and *G. mellonella.* However, table 4 indicates that the percentages of successful development in these two atypical hosts were much lower than those in a usual host, *H. zea,* and did not exceed 21 % in *G. mellonella* and 13 % in *S. frugiperda.* In these two atypical hosts, parasitoid pupation was recorded earlier at 30° than at 25 °C (6-10 days and 14 days, after parasitism, respectively). Percentages of both parasitoid pupation and adult emergence at 30 °C, were higher than at 25 °C. Pupae and adults from parasitoid larvae which developed in *S. frugiperda* or *G. mellonella,* were always smaller than those from the usual host, *H. zea.*

TABLE 4

Pupation and adult emergence of M. croceipes *in* H. zea *and two atypical host species*

Host	Temperature (°C)	Days from parasitization to pupation	Total number of parasitized hosts observed	Percent of parasitoid pupae produced	Percent of emerged adults From total	
					parasitized pupae	parasitized adults
H. zea	25	14-22	60	85.0	90.2	76.7
G. mellonella	25	14-19	87	6.9	50.0	3.4
	30	10-24	81	29.6	70.8	21.0
S. frugiperda	25	14-22	80	12.5	30.0	3.8
	30	6-8	60	15.0	88.9	13.3

DURATION OF PARASITOID DEVELOPMENT

At 25° and 30 °C, the total developmental time of *M. croceipes* in *G. mellonella,* was significantly longer than in *H. zea* (table 5). However, no significant differences were recorded in the developmental time of parasitoid pupae in *G. mellonella* and *H. zea* at either temperature.

DISCUSSION

Development of *M. croceipes* eggs to the germ band stage (Counce & Waddington, 1972) usually occurs in *H. zea,* a typical host, ca. 14 h after oviposition at 26 °C (Greany, 1986). In this study, 85-100 % of the eggs developed to the germ band stage in 1-2 days in both *H. zea* and in the candidate hosts, *G. mellonella, P. interpunctella,* and *P. xylostella ;* however, these high percentages were not related to the percentage of successful parasitization in these hosts. For example, although 100 % of the eggs oviposited in *G. mellonella* and 17 % in *S. frugiperda* attained germ band stage at 30 °C 24-48 h after parasitization, complete parasitoid development occurred in only 21 % and 13 %, respectively, of these

TABLE 5

Duration of development of M. croceipes *in* G. mellonella *and in* H. zea

Temperature (°C)	Host	n	Developmental time (days) (means ± S.D.)		
			From oviposition to pupation	From pupation to adult emergence	Total[1]
25	*G. mellonella*	3	15.7 ± 2.9^{a}	9.3 ± 1.5^{a}	25.0 ± 2.0^{a}
	H. zea	18	10.8 ± 1.4^{b}	8.9 ± 2.5^{a}	20.4 ± 1.6^{b}
30	*G. mellonella*	11	13.0 ± 3.2^{c}	7.3 ± 1.5^{a}	20.3 ± 3.0^{b}
	H. zea	44	8.0 ± 0.7^{d}	7.2 ± 0.9^{a}	15.2 ± 1.1^{c}

[1] Means followed by different letters indicate significant differences as determined by Newman-Keuls multiple-range test at $P < 0.5$.

hosts. Therefore, the percentage of eggs developed to germ band cannot serve as an indicator of overall suitability of the host for the parasitoid.

The incidence of parasitoid egg encapsulation by a host is an important parameter of host suitability (Salt, 1963 ; Bartlett & Ball, 1966 ; Blumberg, 1977 ; Vinson & Iwantsch, 1980 ; Dijkerman, 1990). High frequency of encapsulation may adversely affect parasitoid efficacy in the field (Muldrew, 1953 ; Brewer, 1971 ; Blumberg, 1991) and likewise may cause difficulties in mass rearing of parasitoids (Reed *et al.,* 1968 ; Blumberg, 1977).

Different rates of encapsulation in the various atypical hosts, occurring at different times after parasitism, and under different rearing conditions, may explain the relative importance of encapsulation in preventing successful development of the parasitoid in each of the four hosts studied. Complete encapsulation of *M. croceipes* eggs in *S. exigua* renders this species entirely unsuitable as an alternate host. Apparently, the polydnaviruses present in *M. croceipes* (Stolz *et al.,* 1976 ; Stoltz & Vinson, 1979 ; Stoltz & Guzo, 1986), which prevent encapsulation in typical hosts, were unable to prevent encapsulation of the parasitoid eggs by hemocytes in *S. exigua.* Although encapsulation in *T. ni* was less frequent than in *S. exigua,* it also seems to be a major obstacle to successful development of *M. croceipes* in this host. Some parasitoid larvae that escaped encapsulation were still unable to survive in *T. ni.* This may be due either to encapsulation that occurs in a later stage of the host development (as found in *S. frugiperda* and *G. mellonella*) or to the host itself being nutritionally inadequate. *T. ni* can therefore be considered an unsuitable host for *M. croceipes.*

Host rearing temperature has a significant effect on parasitoid encapsulation in that in both *S. exigua* and *T. ni* a higher incidence of encapsulated eggs occurred on the 2nd day after parasitism at 30 °C than at 25 °C. Host rearing temperature had a significant effect on parasitoid encapsulation in that both *S. exigua* and *T. ni,* was evident on the second day after parasitization. Temperature dependent encapsulation was also reported in the braconid parasitoid *Cardiochiles nigriceps* Viereck and *Heliothis* spp. (Lynn & Vinson, 1977), as well as in several soft scales (Homoptera : Coccidae) and their endoparasitoids (Blumberg, 1982, 1988, 1991 ; Blumberg & DeBach, 1981).

As a host defense mechanism, encapsulation in *S. frugiperda* and *G. mellonella* appears to be less efficient than in *S. exigua* and *T. ni.* First, live and/or dead unencapsulated

M. croceipes larvae were found in parasitized *G. mellonella* and *P. interpunctella* up to 2-4 wk after parasitism. In this same period of time the parasitoid develops to the adult stage in the typical host, *H. zea.* Secondly, the parasitoid was not able to complete development beyond the third instar in *P. interpunctella* even though the larvae were not encapsulated. Finally, although the parasitoid was able to complete development in *G. mellonella,* the percentage was low relative to that in *H. zea.*

The low percentage of successful parasitism in *G. mellonella* and *S. frugiperda,* as well as the smaller size of parasitoid pupae and adults that develop in these two hosts, indicate that the hemolymph of these hosts is probably lacking adequate levels of essential nutrients or specific growth factors (Ferkovich *et al.,* 1991). Another possibility is the production of humoral factors (e.g., ceropins, atacins) by the host that could have inhibited development of the parasitoid embryo (Dunn, 1986).

The main reason for the unsuccessful development of *M. croceipes* in *P. xylostella* is probably the host's size. Larvae of this host, even in their last instar, are probably too small to enable parasitoid growth and development beyond the first instar. Thus, even if no encapsulation occurred and the host was nutritionally adequate for larval development, *P. xylostella* would still be unsuitable as a host for *M. croceipes.*

Although it took *Microplitis* longer to develop and significantly fewer adults were produced in *S. frugiperda* and *G. mellonella* compared with *H. zea,* it may be possible to increase the number of adults emerging from these atypical host species. For example, a higher percentage of adult emergence, and faster development of the parasitoid occurred in *G. mellonella* and *S. frugiperda* at 30 °C compared with that at 25 °C, indicating that manipulation of the rearing temperature of these two hosts may enable higher production of adult *M. croceipes.*

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RÉSUMÉ

Développement et encapsulation de l'endoparasitoïde *Microplitis croceipes* (Hym. : Braconidae) chez six hôtes potentiels (Lepidoptera)

L'encapsulation et le développement de l'endoparasitoïde, *Microplitis croceipes* (Cresson) dont l'hôte habituel est *Helicoverpa zea* (Boddie) ont été étudiés chez 6 autres hôtes possibles. Ces hôtes potentiels sont : *Spodoptera frugiperda* (Smith), *S. exigua* (Hübner), *Trichoplusia ni* (Hübner), *Galleria mellonella* (L.), *Plodia interpunctella* (Hübner) et *P. xylostella* (L.). *S. exigua* et *T. ni* ne permettent pas le développement de *M. croceipes* et les œufs du parasitoïde présentent un fort taux d'encapsulation dans les 3 jours qui suivent leur ponte. L'encapsulation chez *S. frugiperda* se produit principalement au stade œuf du parasitoïde et elle est décelable dès le 6^{e} jour après la ponte à 25° et dès le 2^{e} jour à 30 °C. Chez *G. mellonella,* l'encapsulation ne concerne que la larve du parasitoïde. Chez *P. interpunctella,* les larves du parasitoïde atteignent le 3^{e} stade mais jamais le stade nymphe. Seuls *S. frugiperda* et *G. mellonella* permettent le développement complet de *M. croceipes.* Le pourcentage de parasitoïdes se développant jusqu'au stade adulte est plus élevé à 30 °C qu'à 25 °C (13 % contre 4 % chez *S. frugiperda* et 21 % contre 3 % chez *G. mellonella,* respectivement). Cependant, ces pourcentages ne sont pas assez élevés pour que ces 2 espèces soient de meilleurs hôtes que *H. zea* pour l'élevage de *M. croceipes.*

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